

SEED SIZE, DISPERSAL SYNDROMES, AND THE RISE OF THE ANGIOSPERMS: EVIDENCE AND HYPOTHESIS¹

BRUCE H. TIFFNEY²

The seeds and fruits of angiosperms serve the functions of nurturing, protecting, and dispersing the embryonic plant, and thus form an evolutionarily sensitive portion of the life cycle of the whole organism. Two of these functions also enhance the probability of fossilization of these disseminules. Protection is often achieved through lignification of the fruit or seed wall, predisposing the organ to preservation. Dispersal increases the probability of a propagule arriving at a fossilizing environment. It is, therefore, not surprising that fruits and seeds are a major source of information on the fossil record of the angiosperms, particularly from the Tertiary (Tiffney, 1977a).

This information has generally appeared in descriptive reports of fossil floras and their composition [e.g., the Eocene London Clay Flora (Reid & Chandler, 1933) and the middle Tertiary floras of central Europe (Mai, 1964)]. These floristic studies have formed the basis for synthetic undertakings such as the elucidation of biogeographic patterns (Wood, 1972; Wolfe, 1975; Tiffney, 1980; Mazer & Tiffney, 1982) and the inference of climatic history (Leopold, 1967; Mai, 1970; Friis, 1975; Gregor, 1980a; Collinson et al., 1981). Consideration of evolutionary questions has been largely restricted to the demonstration of species sequences within single genera (e.g., *Stratiotes* L., Chandler, 1923; *Aldrovanda* L., Dorofeev, 1968; *Toddalia* Juss., Gregor, 1979) and families (e.g., Juglandaceae, Manchester & Dilcher, 1981, unpubl. data). However, fruits and seeds additionally offer an excellent starting point for paleobiological inquiry based on modern ecological studies. Of particular note are two considerations: (1) the relation of seed size to the habit and habitat of the parent plant, and (2) dispersal syndromes.

Harper et al. (1970) [after Salisbury (1942)]

have demonstrated a strong correlation between seed weight and the stature and successional status of the parent plant. Herbaceous plants, and those of early successional stages, tend to have small propagules, while dominant forest trees and plants of late successional status tend to have large propagules. Some shrubs and "weedy" trees tend to have propagules of intermediate sizes. The mode of dispersal of a living plant may often be inferred from the morphology of the fruit or seed, together with the mode of its presentation to the dispersal agent (Ridley, 1930; van der Pijl, 1969). While fossilization precludes knowledge of the mode of presentation, many of the morphological characters of the fossils permit inference of the mode of dispersal in at least a broad sense. These two features, propagule size and dispersal, have been examined only in modern plants and generally have been treated separately. In the present paper I extend observations on propagule size and dispersal type through the fossil record and propose that these (1) have been related throughout the history of the angiosperms and (2) underwent an intensive period of change in the latest Cretaceous and early Tertiary. My emphasis will be on propagule size; the subject of dispersal syndromes through time warrants a separate study and is not treated in detail here.

METHODS

In the following discussion, I will use the general term "diaspore" to indicate the reproductive unit that is dispersed or sown. Thus, in the case of a capsule, which releases its contents, the term will apply to the morphological seed. In the case of a drupe or berry, the term will encompass fruit tissue. However, in cases in which reference is

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² Peabody Museum and Department of Biology, Yale University, P.O. Box 6666, New Haven, Connecticut 06511.

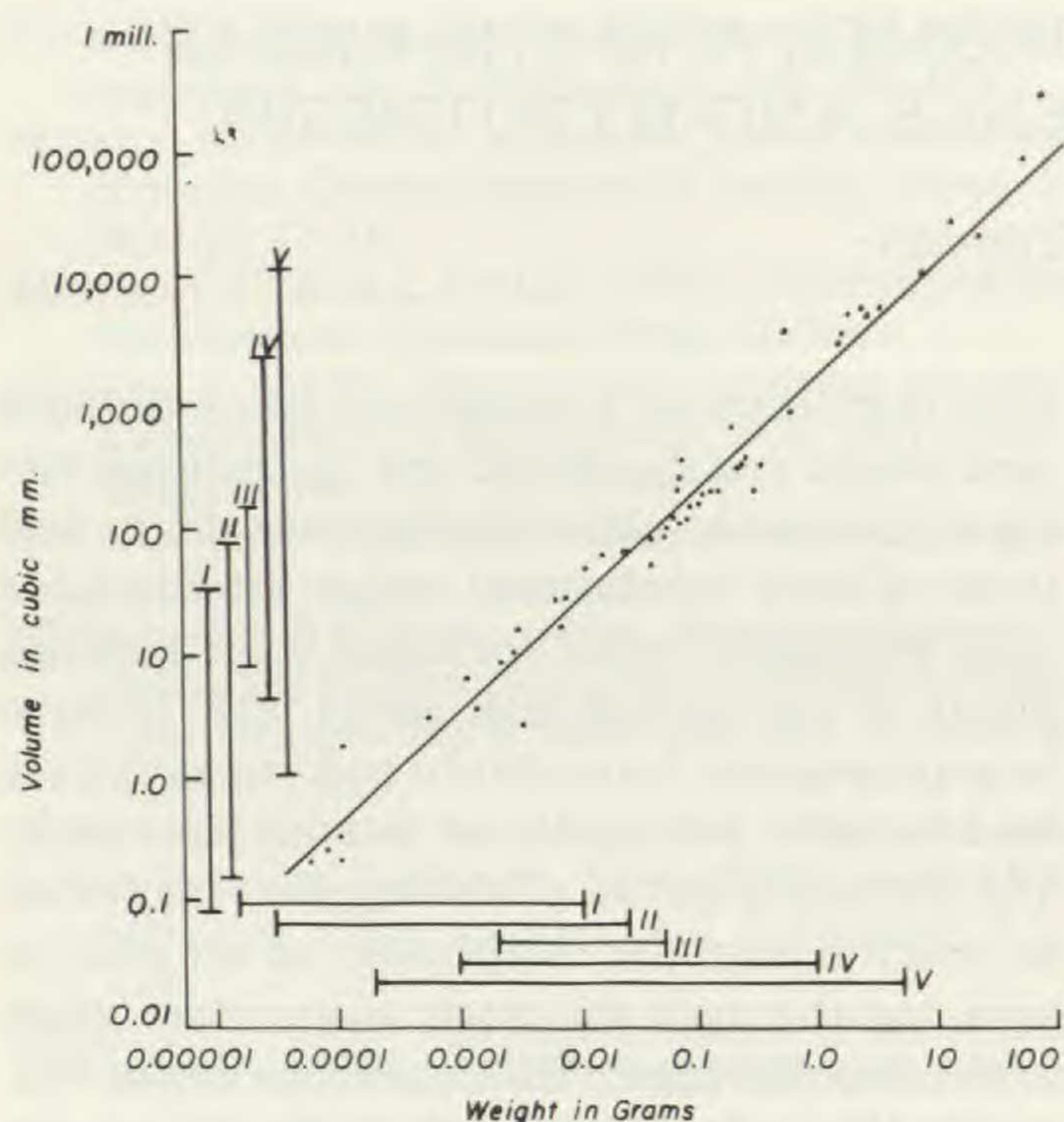


FIGURE 1. Log-log plot of weight versus volume for the propagules of 52 modern angiosperms. The five categories of seed weight (after Harper et al., 1970) on the horizontal axis (weight) are transposed to the vertical axis (volume) by use of the regression line. Categories of plants: I. open habitat; II. woodland margin; III. woodland ground; IV. woodland shrubs; V. woodland trees.

to a specific morphological structure, and particularly when discussing the nutrient reserves of a dispersed seed, I will use the appropriate morphological term.

Salisbury (1942), Harper et al. (1970), and other workers have quantified diaspore size using weight. This approach cannot be applied to a comparative study of fossil seeds because they may be preserved as original organic matter or by replacement with minerals; while lignin has a specific gravity of about 1.2, silicon dioxide has one of 2.65, and pyrite of 5.01. Linear measurements (e.g., length) are also inappropriate because they do not account for variation in three-dimensional shape. I have, therefore, chosen to estimate size from volume. This also permits the calculation of diaspore size from published reports as well as from actual specimens. The use of volume involves two assumptions: (1) that weight and volume are related in fruits and seeds, and (2) that the volumes may be calculated in an accurate and repeatable manner. To test these assumptions, the diaspores of 52 modern species were weighed to the nearest one thousandth of a gram and measured to the nearest tenth of a millimeter. The results are plotted in Figure 1.

A regression of weight versus volume yields $r = 0.928$, indicating a significant correlation between the two. This correlation further suggests that the measurement of volume was sufficiently accurate for the purposes of this study.

Diaspore volumes of seven Cretaceous and 20 representative Tertiary and Quaternary floras were then calculated from specimens and the literature (Table 2). In order to obtain accurate identification and measurement of the individual diaspores, only floras with three-dimensional, well-preserved fossils were used. Volumes were obtained only for those fossils that represented diaspores as defined above. Calculations were based on average width, length, and thickness of the specimens as described. In cases where one or more dimensions were not cited, the missing value(s) was estimated from illustrations. In cases of extreme compaction, thickness was assumed to be a value equal to $0.66 \times$ the width. This value was arrived at empirically, and is an outgrowth of the $2/3$ power law governing the relation of surface area to volume. The volume of spherical diaspores was estimated at $4/3\pi r^3$. On those occasions where spines or other projections seriously hampered accurate measurement, estimates were made of the volume. The stratigraphic ages of the deposits are those provided by the authors, with modification in light of recent data (Gregor, 1980b) as appropriate. The conversion of stratigraphic age to absolute age is made from van Eysinga (1975) and Gregor (1980b). Assignment of absolute age is necessary to permit calculation of regression values and aids in the relative location of the floras. However, the ages are *approximate* and should be recognized as such. Regression values were calculated using a pre-programmed Texas Instruments TI-55 calculator. Readers are cautioned that the use of numbers with regard to these fossils may convey a false sense of precision. While the numbers used are certainly valid within the relative framework of the present discussion, they often involve subjective judgements and should be regarded as educated approximations, not as absolutes.

DATA

CRETACEOUS FRUITS AND SEEDS

The consideration of Cretaceous fruits and seeds falls into two sections, since floras of three-dimensional fruits and seeds have, to date, only been found in the Late Cretaceous. Before this

time, the record of angiosperm reproductive structures involves isolated fossils.

A summary of the better documented fruits and seeds of Early Cretaceous and Cenomanian age (115–95 million years ago, henceforth Ma) is presented in Table 1. The majority of these are preserved as casts or impressions; of the compressions, only a few can be or have been studied in anatomical detail. As a result, many of the earliest reported forms cannot be clearly assigned to the angiosperms and may well be gymnospermous. This has been suggested in the case of *Onoana californica* Chandl. & Axelr. (Chandler & Axelrod, 1961), and by inference *Onoana nicanica* Krass. (Krassilov, 1967), by Wolfe et al. (1975). The same arguments apply to several other Early Cretaceous endocarp-like forms including "*Carpolithus*" (Chandler, 1958), *Nyssidium* Saml. (Samylina, 1961), *Prototrapa* Vas. (Vasil'yev, 1967), *Araliaecarpum* Saml. and *Caricopsis* Saml. (Samylina, 1960) and *Knella* Saml. (Samylina, 1968). Retallack and Dilcher (1981) have similarly viewed many of the above reports as potentially non-angiospermous. These reports will not be considered further.

The remaining reports tabulated in Table 1 fall into two categories. The first includes several structures reported by Fontaine (1889) under the genus "*Carpolithus*" and interpreted by Dilcher (1979) and Retallack and Dilcher (1981) to represent multifollicles. I have not personally examined these specimens and accept the judgment of these authors. The second category includes well-preserved fruits, often containing seeds. These involve clearly angiospermous material such as *Caspiocarpus paniculiger* Vach. & Krass. (Vachrameev & Krassilov, 1979), *Ranunculaecarpus quinquicarpellatus* Saml. (Samylina, 1960), *Carpites liriophylli* Lesq. (Dilcher et al., 1976) and a host of forms from the Dakota Formation of central North America.

The majority of these Early Cretaceous angiosperm fruits are small, individual carpels ranging from 1 to 15 mm in length and from 0.5 to 8 mm in width, or are capsules of from 10 to 12 mm in diameter. In the five cases where seeds are known from these fruits, the seeds are small, ranging from 0.2 mm³ (*Caspiocarpus paniculiger*) to approximately 7.5 mm³ (estimated for the "unpublished five-carpellate fruit" from the Dakota Group; Dilcher, 1979). The one exception to this tendency to small size is *Carpolithus curvatus* Font., which is a carpel about 40 mm long and 15 mm wide. This specimen is not well pre-

served, and there is no indication as to the size of the included seeds.

The most common fruit morphology is a dehiscent follicle, borne on a central axis, although capsules are also frequently observed. This is in keeping with the classic hypothesis that the conduplicate carpel, and dispersal by morphological seeds, are the primitive conditions in the group (Cronquist, 1968; Takhtajan, 1969). The one potential exception to this pattern is the report of a fleshy fruit from the Cenomanian (98 Ma; Dilcher, 1979). However, the status of this fossil is not clear because Retallack and Dilcher (1981: 49) imply that no fleshy fruits are known from Cenomanian and older sediments. The reported seeds are all apparently thin-walled and without any distinctive features related to dispersal. The capsular-follicular morphology of the fruits and the small, unspecialized, nature of the seeds are characters indicative of a general adaptation to abiotic dispersal mechanisms, a conclusion also reached by Retallack and Dilcher (1981).

Individual fruits are also reported in the Late Cretaceous, often as constituents of compression or impression leaf floras, and several reports exist of isolated occurrences of seeds or seed-like objects (Miner, 1935; Schemel, 1950; Hall, 1963, 1967; Binda, 1968; Colin, 1973; Knobloch, 1981). However, of greater importance to the present work are several fairly diverse (10–50 species) floras of three dimensionally preserved fruits and seeds from fluvial and lacustrine sediments. The most important of these are listed in rows 1–7 of Table 2; several others of lower diversity have not been included but are of a similar nature (Knobloch, 1971, 1977). Although some of these seeds have been assigned to extant families (Caryophyllaceae, Cyperaceae, Menispermaceae, Myricaceae, Theaceae, Urticaceae; Knobloch, 1977; Jung et al., 1978) and orders (Juglandales; Friis, 1984), the majority have been placed in the organ genus *Microcarpolithes* Vangerow erected for seeds or one-seeded fruits of angiospermous affinities. [This genus requires re-naming. The type species, *M. hexagonalis* Vangerow (Hall, 1963) has been shown to be an insect coprolite (Knobloch, 1977).]

The average size of the seeds in these floras is approximately 1.7 mm³ (see Table 2, column $\bar{x}$ and Fig. 2, floras 1–7). This small size does not appear to be a function of mechanical sorting, or of ecological separation, for a variety of reasons. The Santonian-Campanian floras (about 77 Ma) reported by Friis (1984) from Åsen, Sweden, and

TABLE 1. Summary of individually reported fruits and seeds of presumed angiospermous affinities from Early Cretaceous and Cenomanian localities. Judgement of angiospermous affinities in the "comment" column is by the present author unless otherwise noted. "No distinguishing angiospermous features" only implies that the specimen is not *clearly* angiospermous.

Age ^a	Name	Locality	Type	Size	Reference	Comment
Tithonian-Berrasian (134)	" <i>Tyrmocarpus</i> "	Tyrma R., Siberia	"capsule-like fruit"	ca. 6 mm diam.	Krassilov (1973) Hughes (1976)	No distinguishing angiospermous features.
Valangian (127)	<i>Carpolithus</i>	Vaucluse, France	unclear	22 mm × 12 mm	Chandler (1958)	The original (now lost) was a sandstone cast with no distinctively angiospermous features.
Barremian (117) ^b	<i>Nyssidium orientale</i> Sam.	Siberia, U.S.S.R.	unclear—inferred as endocarp	10 mm × 6 mm	Samylina (1961)	No distinguishing angiospermous features. Illustrated specimens show little relation to <i>Nyssa</i> . Found in a totally gymnospermous flora. ^a
Barremian (117) ^b	<i>Nyssidium</i> Sp.	Siberia, U.S.S.R.	unclear—inferred as endocarp	10 mm × 5 mm	Samylina (1961)	
Barremian (117) ^b	<i>Onoana californica</i> Chand. & Axelr.	California, U.S.A.	unclear—inferred as endocarp	20 mm × 15 mm	Chandler and Axelrod (1961)	No distinguishing angiospermous features (Wolfe et al., 1975). ^c
Late Barremian-Early Aptian (112) ^d	<i>Carpolithus geminatus</i> Font.	Virginia, U.S.A.	multifollicle	6 mm × 9 mm ^e	Fontaine (1889)	Footnote f.
Late Barremian-Early Aptian (112) ^d	<i>Carpolithus sessilis</i> Font.	Virginia, U.S.A.	multifollicle	12 mm × 4 mm	Fontaine (1889)	Footnote f.
Late Barremian-Early Aptian (112) ^d	<i>Carpolithus virginianensis</i> Font.	Virginia, U.S.A.	multifollicle	7–10 mm × 4–6.5 mm	Fontaine (1889)	Footnote f.
Aptian (110)	<i>Onoana nicanica</i> Krass.	Primorye, U.S.S.R.	unclear—inferred as endocarp	8–10 mm × 5.5–7.5 mm	Krassilov (1967)	No distinguishing angiospermous features (cf. Wolfe et al., 1975). Preservation poor. ^c
Aptian-Albian (107.5)	<i>Prototrappa douglasi</i> Vass.	Victoria, Australia	endocarp	1–3 mm × 0.5–1.5 mm	Vasil'yev (1967)	Resemblance to <i>Trapa</i> is superficial; angiospermous affinities unclear. Impression.

TABLE 1. (Continued).

Age ^a	Name	Locality	Type	Size	Reference	Comment
Aptian-Albian (107.5)	<i>Prototrappa prae-pomelii</i> Vass.	Victoria, Australia	endocarp	2 mm × 1 mm	Vasil'yev (1967)	Resemblance to <i>Trapa</i> is superficial; angiospermous affinities unclear. Impression.
Aptian-Albian (107.5)	<i>Prototrappa tenuirostrata</i> Vass.	Victoria, Australia	endocarp	1.2 mm × 0.5 mm	Vasil'yev (1967)	Resemblance to <i>Trapa</i> is superficial; angiospermous affinities unclear. Impression.
Albian (105) ^b	<i>Araliaecarpum kolymensis</i> Sam.	Siberia, U.S.S.R.	unclear; possibly a winged endocarp?	6 mm × 6 mm	Samylina (1960)	Affinities unclear to present author.
Albian (105) ^b	<i>Caricopsis compacta</i> Sam.	Siberia, U.S.S.R.	unclear	3–5 mm × 2 mm	Samylina (1960)	Affinities unclear to present author.
Albian (105) ^d	<i>Carpolithus conjugatus</i> Font.	Virginia, U.S.A.	multifollicle	7.5 mm × 3.6 mm ^e	Fontaine (1889)	Footnote f.
Albian (105) ^d	<i>Carpolithus curvatus</i> Font.	Virginia, U.S.A.	multifollicle	42 mm × 14.2 mm ^e	Fontaine (1889)	Footnote f.
Albian (105) ^d	<i>Carpolithus fasciculatus</i> Font.	Virginia, U.S.A.	multifollicle	15 mm × 8 mm ^e	Fontaine (1889)	Footnote f.
Albian (105) ^d	<i>Carpolithus ternatus</i> Font.	Virginia, U.S.A.	multifollicle	8–11 mm × 4–7 mm ^e	Fontaine (1889)	Footnote f.
Albian (105) ^e	<i>Carpolithus karatscheensis</i> Vachr.	Kazakhstan, U.S.S.R.	multifollicle	—	Vachrameev (1952)	Original article not seen; data from Retallack and Dilcher (1981).
Albian (105)	<i>Caspiocarpus paniculiger</i> Vachr. & Krass.	Kazakhstan, U.S.S.R.	dehiscent follicle	Fruit—1 mm × 0.5 mm Seed—0.8 × 0.5 mm	Vachrameev and Krassilov (1979)	Clear angiospermous affinities.
Albian (105) ^b	<i>Knella harrisiana</i> Sam.	Kolyma R., U.S.S.R.	unclear—endocarp?	16 mm × 5 mm	Samylina (1968)	Poor preservation, angiospermous affinities not demonstrated. See also Hughes (1976). ^c

TABLE 1. (Continued).

Age ^a	Name	Locality	Type	Size	Reference	Comment
Albian (105) ^b	<i>Ranunculaecarpus quinquecarpellatus</i> Sam.	Kolyma R., U.S.S.R.	Dehiscent follicle	Fruit—10 mm × 5 mm × 2 mm Seed—1.5 mm × 0.6 mm	Samylina (1960)	Angiospermous affinities fairly certain.
Cenomanian (97.5)	<i>Carpites liriophylli</i> Lesq.	Dakota Group, U.S.A.	Dehiscent follicle	Fruit—15–20 mm × 3–4 mm Seed—1.4 mm × 0.6 mm	Dilcher et al. (1976); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	<i>Carpites tiliaceus</i> Lesq.	Dakota Group, U.S.A.	Five-valved capsule	ca. 10 mm diam. ^h	Lesquereux (1892); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	<i>Laurus macrocarpa</i> Lesq.	Dakota Group, U.S.A.	Syncarpous fruit	12 mm × 8.3 mm ^h	Lesquereux (1874); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	<i>Platanus primaeva</i> Lesq.	Dakota Group, U.S.A.	Spherical mass of individual fruits	head ca. 3–4 mm diam. ^h	Lesquereux (1892); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	" <i>Salix</i> "	Dakota Group, U.S.A.	Dehiscent follicle	3.3 mm × 1.5 mm ^h	Lesquereux (1892); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	un-named	Dakota Group, U.S.A.	Fleshy fruit	5–6 mm diam. ^h	Dilcher (1979)	Dilcher (1979) interprets as angiospermous.

TABLE 1. (Continued).

Age ^a	Name	Locality	Type	Size	Reference	Comment
Cenomanian (97.5)	"unpublished 5-carpellate fruit" ⁱ	Dakota Group, U.S.A.	Five-valved capsule	Fruit—10 mm diam. Seeds—3.3 mm × 2.5 mm × 1.2 mm ⁱ	Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	"un-named follicular axis associated with <i>Magnoliaephyllum</i> "	Dakota Group, U.S.A.	Dehiscent follicle	Fruit—2.7 mm × 2.0 mm Seed—0.8 mm × 0.5 mm ^h	Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	"un-named globose heads"	Dakota Group, U.S.A.	Globose mass of individual fruits	Head ca. 10 mm × 7.5 mm diam. ^h	Dilcher (1979)	Fairly clear angiospermous affinities.
Cenomanian (94)	Platanaceae	Dakota Group, U.S.A.	Spherical mass of individual fruits	Not given	Schwarzwalder and Dilcher (1981)	Infructescences and leaves demonstrably related to Platanaceae.

^a Absolute ages after van Eysinga (1975).

^b Age after Hughes (1976).

^c Retallack and Dilcher (1981) consider the angiospermous affinities of this species to be unproven.

^d Age after Doyle and Hickey (1976).

^e Measurements are approximate; made from Fontaine's (1889) illustrations.

^f The identification of this species as a multifollicle is provided by Retallack and Dilcher (1981), although Fontaine (1889) placed it as a seed of a gymnosperm. I have not viewed this material.

^g Age after Vachrameev and Krassilov (1979).

^h Measurements are approximate; made from Dilcher's (1979) illustrations.

ⁱ This unpublished specimen may be the same as *Carpites tiliaceus* Lesq. (Dilcher, 1979). Since the measurements given for both seed and fruit are made from Dilcher's illustrations, they must be viewed as approximate. The measurements for the seed are taken from the presumed seed-cavity cast.

TABLE 2. Data on individual Late Cretaceous and Tertiary fruit and seed floras. N = total number of seeds measured in flora, $\bar{x}$ = average value, s.d. = standard deviation, CV = covariance.

Stratigraphic Age	Estimated Numeric Age ^a	Locality	Reference	N	$\bar{x}$ (mm ³)	s.d.	Co. var. (s.d./ $\bar{x}$)	Largest (mm ³)	Smallest (mm ³)
1. Santonian-Campanian	77	Åsen, Sweden	Friis (1984)	>50	—	—	—	27 ^b	0.02 ^b
2. Santonian-Campanian	77	Gay Head, Massachusetts, U.S.A.	Tiffney (unpubl. data)	41	5.7	10.5	1.82	55	0.03
3. Santonian-lower Campanian	77	Staré Hamry 1, Czechoslovakia	Knobloch (1977)	19	1.4	0.7	0.5	3	0.41
4. Senonian	75 ^c	Aachen, West Germany	Vangerow (1954)	11	0.2	0.17	0.83	0.5	0.03
5. Senonian	75 ^c	Petrovice, Czechoslovakia	Knobloch (1964)	11	0.3	0.2	0.625	0.73	0.11
6. Campanian-Early Paleocene	73–63? ^d	Horní, Bečva, Czechoslovakia	Knobloch (1977)	29	1.5	1.4	0.91	6.4	0.15
7. Late Senonian	69	Kössen, Austria	Knobloch (1975)	9	1.3	0.9	0.69	3	0.15
8. Late Senonian	69	Kössen, Austria	Jung et al. (1978)	13	1.5	1.2	0.82	3	0.15
9. Maastrichtian-Middle Paleocene	67–61? ^d	Rusava, Czechoslovakia	Knobloch (1977)	20	1.2	0.8	0.66	3	0.06
10. Late Paleocene	55	Woolwich and Reading Beds, England	Chandler (1961)	18	129	234	1.82	731	1.2
11. Ypresian (Early Eocene)	52	London Clay, England	Reid and Chandler (1933)	202	1,957	5,932	3.03	61,318	0.25
12. Lutetian (Middle Eocene)	45	Geiseltal, East Germany	Mai (1976)	25	308	643	2.1	3,182	2.1
13. Auversian (Late Eocene)	42	Clarno, Oregon, U.S.A.	Scott (1954); Bones (1979)	33	3,729	10,626	2.8	59,150	0.25
14. Middle Oligocene	32	Haselbach, East Germany	Mai and Walther (1978)	79	268	1,220	4.5	9,294	0.07
15. Middle Oligocene	30	Bovey Tracey, England	Chandler (1957)	33	68	225	3.3	1,300	0.35
16. Late Oligocene	25	Tomsk, Siberia U.S.S.R.	Nikitin (1965)	95	19	123	6.4	1,200	0.07
17. Lower to Middle Ottnangian (Lower Miocene)	18.5	Chomutov-Most-Teplice Basin, Czechoslovakia	Bůžek and Holý (1964)	22	19	38.6	2	180	1.27

TABLE 2. (Continued).

Stratigraphic Age	Estimated Numeric Age ^a	Locality	Reference	N	$\bar{x}$ (mm ³)	s.d.	Co. var. (s.d./ $\bar{x}$)	Largest (mm ³)	Smallest (mm ³)
18. Lower Miocene	18	Rusinga, Kenya	Chesters (1957)	29	1,319	2,044	1.6	10,935	63
19. Middle Ottnangian (Lower Miocene)	18	Wiesa, East Germany	Mai (1964)	71	1,410	3,263	2.3	15,611	0.25
20. Middle to Upper Ottnangian (Lower Miocene)	18	Hartau, East Germany	Mai (1964)	51	774	2,303	3	11,600	1
21. Upper Ottnangian (Lower Miocene)	17.5	Turów, Poland	Czeczott and Skirgiello (1959, 1961a, 1961b, 1967, 1975, 1980a, 1980b)	47	2,501	4,340	1.7	15,096	2
22. Carpathian (Lower Miocene)	17	Nowy Sącz Basin, Poland	Zancucka-Środoniowa (1979)	79	7	22.8	3.3	179	0.014
23. Badenian (Middle Miocene)	14.5	"Gdów Bay," Poland	Zancucka-Środoniowa (1966)	52	95	366	3.9	2,125	0.04
24. Pliocene	3.5	Kranichfeld, East Germany	Mai (1965)	35	13	63	5	1,215	0.1
25. Pliocene	3.5	Bergheim, West Germany	van der Burgh (1978)	83	100	245.5	2.5	1,400	0.9
26. Plio-Pleistocene	1.8	Rippersroda, East Germany	Mai et al. (1963)	66	68.1	301	4.4	2,125 ^e	0.014
27. Holocene	0.035 0.068	New Haven, Connecti- cut, U.S.A.	Pierce and Tiffney (unpubl. data)	43	1,077	4,116	3.8	25,000 ^f	1.1

^a Numerical ages after van Eysinga (1975), millions of years (Ma).

^b Estimated from absolute possible smallest and largest sizes of angiosperm fruiting remains presented in Friis (1984). The largest fruiting remain is a seed-bearing fruit (Friis, pers. comm.) and is likely not the unit of dispersal.

^c Deposit cited as "Senonian;" 75 Ma is taken as the midpoint of the Senonian.

^d Exact stratigraphic position of deposit not determined; possible range indicated.

^e This value is for a nut of *Corylus*.

^f Value for *Juglans cinerea*; the next largest value is 8,000 mm³ for *Carya*.

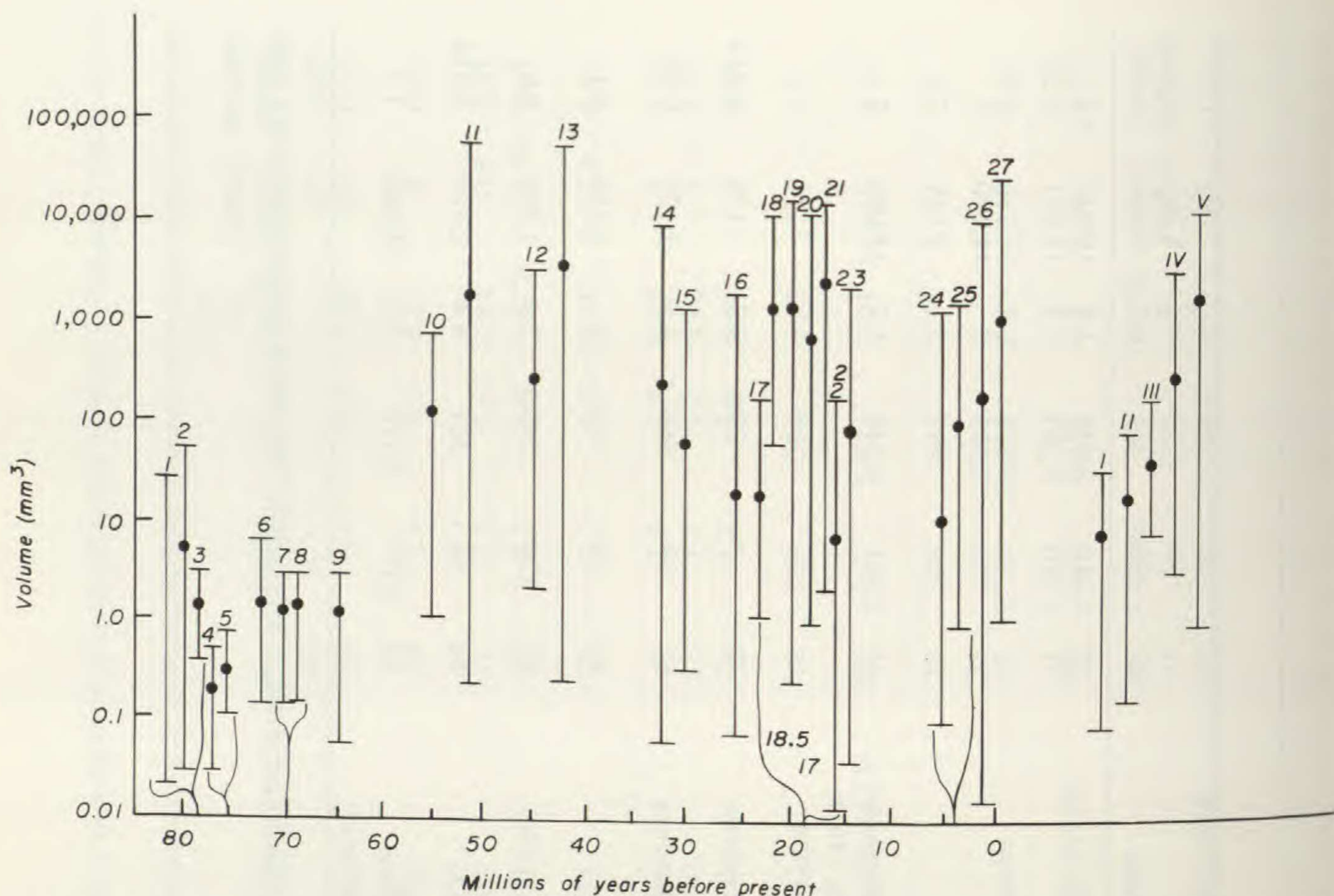


FIGURE 2. Plot of seed volume (vertical axis, logarithmic) versus time (horizontal axis) for 27 Cretaceous and Tertiary fruit and seed floras. The vertical line for each flora indicates the range of diaspore volume; the central dot, the average diaspore volume. The lines I-V at the far right correspond to the volume equivalents of the ecological classes of Harper et al. (1970) as derived in Figure 1. (I. Open habitat; II. woodland margins; III. woodland ground; IV. woodland shrubs; V. woodland trees.) Note that the average volume is not available for flora #1, and that in several cases (floras 1-3, 7, 8, 17-22, 24, 25), more than one flora occurs at a single time.—1. Åsen, Sweden (Friis, 1984).—2. Gay Head, Massachusetts, U.S.A. (Tiffney, unpubl. data).—3. Staré Hamry 1, Czechoslovakia (Knobloch, 1977).—4. Aachen, West Germany (Vangerow, 1954).—5. Petrovice, Czechoslovakia (Knobloch, 1964).—6. Horní Bečva, Czechoslovakia (Knobloch, 1977).—7. Kössen, Austria (Knobloch, 1975).—8. Kössen, Austria (Jung et al., 1978).—9. Rusava, Czechoslovakia (Knobloch, 1977).—10. Woolwich and Reading beds, England (Chandler, 1961).—11. London Clay, England (Reid & Chandler, 1933).—12. Geiseltal, East Germany (Mai, 1976).—13. Clarno, Oregon, U.S.A. (Scott, 1954; Bones, 1979).—14. Haselbach, East Germany (Mai & Walther, 1978).—15. Bovey Tracey, England (Chandler, 1957).—16. Tomsk, Siberia, U.S.S.R. (Nikitin, 1965).—17. Chomutov-Most-Teplice Basin, Czechoslovakia (Bůžek & Holý, 1964).—18. Rusinga, Kenya (Chesters, 1957).—19. Wiesa, East Germany (Mai, 1964).—20. Hartau, East Germany (Mai, 1964).—21. Turów, Poland (Czeczott & Skirgiello, 1959, 1961a, 1961b, 1967, 1975, 1980a, 1980b).—22. Nowy Sącz Basin, Poland (Zancucka-Środoniowa, 1979).—23. "Gdów Bay," Poland (Zancucka-Środoniowa, 1966).—24. Kranichfeld, East Germany (Mai, 1965).—25. Bergheim, West Germany (van der Burgh, 1978).—26. Rippersroda, West Germany (Mai et al., 1963).—27. New Haven, Connecticut, U.S.A. (Pierce & Tiffney, unpubl. data).

by Tiffney (unpubl. data, see Tiffney, 1977b) from Massachusetts, U.S.A., are both in fluvial deposits containing large pieces of wood and, in the case of Tiffney's material, conifer cones (Miller & Robison, 1975). The same situation exists in lagoonal sediments of a similar age from Cliffwood Beach, New Jersey, U.S.A. (Tiffney, unpubl. data). Thus, the size of the angiosperm reproductive remains from these deposits cannot be explained by mechanical sorting.

It is possible that a uniformly small seed size could result from the derivation of the fossils

from a single, ecologically-specialized aquatic community, or a combination of aquatic and river-floodplain communities. At the outset, it is noteworthy that in one case (Petrovice, Czechoslovakia, flora #4) Knobloch (1964) described a seed flora of 11 species of *Microcarpolithes* comparable in all respects with other central European Cretaceous fruit and seed floras, but in the same sample as a flora of large leaves including *Araliophyllum* sp. Ett., *Debeya bohemica* Knob., *Pseudoprotophyllum senonense* Knob., *Quercophyllum triangulodentatum* Knob., *Laurophyl-*

lum elegans Holl., *Proteophyllum* sp., *Platanophyllum* sp., *Cinnamomophyllum* sp., and three species of *Dicotylophyllum*. This clearly suggests that at least some of these seeds were borne by woody, nonaquatic vegetation. The question remains, do these floras sample only unstable floodplain forests? The answer lies in an examination of Tertiary and modern deposits, where we have a better idea of the community affinity of the fossils through their taxonomy. The fluvial deposits of the Tertiary (e.g., Bergheim, or those described by Gregor, 1978, 1980b) often include a wide range of fruit and seed sizes that are presumed on taxonomic grounds to be derived from several separate communities, including upland mesic ones. This is further supported by the New Haven, Connecticut flora (#27), which is of Holocene age and includes many upland taxa. Even those Tertiary floras least affected by transport include occasional samples of plants growing in the mesic sites surrounding the water. For example, the Oligocene (30 Ma) lacustrine Bovey Tracey flora of England (Chandler, 1957) includes larger seeds of such trees as *Magnolia* L., *Fagus* L., and *Nyssa* Gronov. ex L. In conclusion, it seems unlikely that these Cretaceous floras are solely records of aquatic or floodplain vegetation.

The morphology of these Late Cretaceous fruits and seeds is somewhat more diverse than that of the Early Cretaceous and Cenomanian remains. Follicles and capsules are still common (Massachusetts and New Jersey deposits), but some evidence is at hand for nuts and drupes (Friis, 1984; Tiffney, unpubl. data). While many of the seeds in these deposits have thin or fragile walls, others have rather thick walls and well-developed surficial sculpture. The dehiscent fruits and thin-walled small seeds suggest the continuing importance of abiotic dispersal mechanisms. However, the presence of drupes and seeds with thick walls is circumstantial evidence for at least the potential for adaptation to animal dispersal, if not for its presence in a limited degree.

Exceptions exist to the general rule of small Cretaceous diaspores. Monteillet and Lappartient (1981) reported a Late Campanian to Maastrichtian (70–66 Ma) flora from Senegal, including seven species of angiosperm fruits with an average volume of 51,950 mm³. The fossils are poorly preserved, and in the cases of "*Annona*" L., "*Cola*" Schott, and perhaps "*Cordyla*" Lour. and "*Trichilia*" P.Br., I am not convinced that the specimens are of plants. The illustrated spec-

imens of *Borassus* L., *Meliacea* (? new form genus), and perhaps *Nauclea* L. are more convincing. Chesters (1955) has also reported large fruits of Annonaceae, Icacinaceae, and possible other angiosperms from the Maastrichtian (68 Ma) of Nigeria. Although large fruit size is no guarantee of large seed size (*Nauclea* has tiny seeds, Willis, 1973); it appears that larger diaspores were becoming more common in the late Cretaceous.

TERTIARY FRUITS AND SEEDS

Individual large diaspores are known from the Paleocene (Brown, 1962; Koch, 1972a, 1972b), but the only published fruit and seed floras are those of the Woolwich and Reading beds of southern England and possibly Horní Bečva and Rusava, Czechoslovakia. The Rusava flora (Knobloch, 1977) is between latest Cretaceous (67 Ma) and middle Paleocene (60 Ma) in age, while Horní Bečva is inferred from Table 1 of Knobloch (1977) as being between Campanian (73 Ma) and Early Paleocene (63 Ma) in age. Both floras are quite similar to those of Staré Hamry I and Petrovice, to which they are geographically close.

By contrast, the flora of the Late Paleocene (55 Ma) Woolwich and Reading beds (Chandler, 1961) includes a diverse array of large and small diaspores with an average volume of 129 mm³. This sets the pattern for the remaining Tertiary floras, which vary in percentage composition of larger and smaller diaspores, but which always include both. The basic trends can be discerned from columns " $\bar{x}$," "largest diaspore," and "smallest diaspore" in Table 2, and from floras 10–27 of Figure 2. Very large diaspores first appear in numbers in the Early Eocene (52 Ma) London Clay flora and dominate the Middle Eocene (45–42 Ma) Geiseltal and Clarno floras and the mid-Oligocene (32 Ma) Haselbach flora, resulting in high average diaspore sizes for these floras. From the Late Oligocene, there is a general tendency for the average diaspore size of a flora to decrease through Pliocene/Pleistocene time, although this trend is not statistically significant. This decrease in average diaspore size is not due to a decrease in the size of the largest diaspores in each flora (by regression of largest seed size versus age ($P = 0.1$; $r = 0.40$, $N = 18$), but to the occurrence of fewer large diaspores in each flora.

Herbaceous angiosperms began to diversify dramatically in the latest Paleogene and the early Neogene (Tiffney, 1981). Herbs normally have

small seeds (Harper et al., 1970), and their increasing importance during this time is reflected in the reduced average diaspore volumes of the floras commencing with the Lagernogo Sad deposit (Tomsk, Siberia; age from Dorofeev, 1963) and carrying through the later Tertiary floras from the Chumotov-Most-Teplice basin (Czechoslovakia), Nowy Sącz basin (Poland), and Kranichfeld (East Germany). While the average diaspore volume (ADV) of these floras is small relative to that of other Tertiary floras, it is markedly larger than the ADV of the Cretaceous floras. The large average volumes for the Miocene Gdów Bay (Poland) and Pliocene Rippersroda (East Germany) floras are due to the presence of a few large diaspores. Deletion of *Corylus* L., *Fagus* L., and *Carya* Nutt. from the former flora brings the average volume down to 9.2 mm³, and deletion of *Trapa* L. and *Corylus* L. from the Rippersroda flora brings the average volume down to 21.5 mm³. The large average volume for the Pliocene Bergheim flora (Mine Fortuna-Garsdorf 1) of West Germany results from the river sands of this deposit having a large allochthonous component derived from upland forest trees (e.g., *Magnolia* L., *Persea* Mill., *Corylus* L., *Castanea* Mill., *Quercus* L., *Halesia* J. Ellis ex L., *Styrax* L.). In spite of these individual differences in ecological and taphonomic setting, it is interesting that each of these floras shows a greater range of diaspore size and a higher average diaspore volume than the Cretaceous floras.

The dispersal mechanisms and syndromes of Tertiary angiosperm fruits and seeds may be inferred from their morphology and from their living relatives. Neither source is totally satisfactory; many morphological features are not preserved, and present dispersal adaptations of a genus or family are no guarantee of past mechanisms. However, both lines of evidence suggest that a wide range of fruits and seeds adapted to animal dispersal were present by the Eocene and Oligocene. This included a variety of sizes from the smaller berries of the Vitaceae to the larger aggregate fruits of the Annonaceae or the drupes of the Mastixiaceae. This diversity of fruit types and sizes offered opportunities to a range of dispersal agents, but particularly to those able to deal with larger disseminules. With the Miocene diversification of herbaceous angiosperms (Retallack, 1981; Tiffney, 1981), an array of small seeds and fruits became available, which was probably important to ground-dwelling rodents and granivorous birds. Thus, the Tertiary ap-

pears to be the time in which major dispersal patterns (diaspore morphologies, relations with particular agents) first achieved their modern form and diversified among angiosperms.

SUMMARY

Cretaceous diaspores are generally small. Cretaceous seed floras are marked by a small average diaspore volume (ADV) and a limited range of diaspore volume (RDV). Early Tertiary floras exhibit a major increase in ADV. Succeeding floras show a broad trend of decreasing ADV, but with no decrease in RDV. The change in ADV through the Tertiary is a result of changes in the relative proportions of large and small diaspores in each flora. Small diaspores show no trend in size change through the Cretaceous and Tertiary, and after their appearance in the Tertiary, large diaspores also show no trend in size change. The increase in diaspore size is paralleled by an apparent change from the dominance of abiotic dispersal mechanisms in the Cretaceous to the increasing importance of biotic dispersal agents commencing in the earliest Tertiary.

This pattern of change in size and mode of dispersal cannot be ascribed to taphonomic or ecologic factors because similar depositional environments are sampled in both Cretaceous and Tertiary deposits. Certainly the deposits of Åsen and Massachusetts demonstrate that larger fruits and seeds could have been carried into the deposit and preserved if present. Many of the Tertiary deposits (e.g., Nowy Sącz, Kranichfeld) demonstrate that even deposits dominated by aquatic vegetation may be expected to include some elements of mesic communities.

Climate could have influenced the composition of the vegetation or the presence of dispersal agents. However, Cretaceous climates from the first appearance of the angiosperms through to the latest Cretaceous are generally felt to have been as warm as those of the early Tertiary (Savin, 1977; Barron et al., 1981; Thompson & Barron, 1981), although there is good evidence for a latest Cretaceous-Paleocene cool phase (Hickey, 1981). In addition, the European Pliocene and Quaternary include climates that were cooler than those of any period of angiosperm history, but floras from these epochs have at least a few large diaspores. Perhaps the only unanswerable bias is that all the fruit and seed data are derived from northern hemisphere, primarily European, localities. It is possible that different patterns in

the evolution of diaspore size could have taken place in other portions of the world, but this cannot be evaluated from existing paleontological data. However, extant tropical (Levin, 1974) and temperate (Salisbury, 1942; Harper et al., 1970) angiosperm fruits and seeds apparently exhibit the same range of sizes.

The timing of this transition from small to large diaspores, and from the dominance of abiotic dispersal to the increased importance of biotic dispersal, is not clear from present knowledge. Since the mid- to Late Cretaceous and the early to mid-Tertiary of Europe both possessed warm climates, they presumably had a similar potential to host tropical plants. If plants with large diaspores were present in the Cretaceous tropics, they should have been seen in the European Cretaceous, much as they were in the Tertiary. However, a Cretaceous-Tertiary boundary cooling at higher latitudes (Hickey, 1981) could have masked the evolution of angiosperms with large diaspores in the tropics in the latest Cretaceous. These could have then appeared in northerly latitudes with the return of subtropical climates in the early Tertiary.

INTERPRETATIONS

The observed pattern in seed size can be explained most simply as a response to one or both of two ecological factors. The first is the relation between seed size and the habit or ecological site of the parent plant. The second is the importance of dispersal agents, which exert pressure on the morphology and size of fruits and seeds, as evidenced by the existence of distinct "dispersal syndromes" in the angiosperms (van der Pijl, 1969). Each of these factors will be treated in turn.

SEED SIZE AND PARENT PLANT HABIT/HABITAT

Harper et al. (1970) and Silvertown (1981), following on the classic work by Salisbury (1942), have demonstrated a correlation between the habit, habitat, and diaspore weight of individual plants. Short-lived or weedy plants of open or unstable habitats generally have many small diaspores that may be dispersed widely, often by abiotic mechanisms (wind, water). These seeds provide very little nutrient reserve to the germinating seedling, so that seedlings generally survive only in open, sunny habitats. However, the large numbers and wide dispersal of these diaspores increase the likelihood that a few seedlings

will germinate in suitable habitats. At the other end of the scale, dominant, long-lived, forest trees of large stature tend to bear fewer, larger diaspores, often involving large seeds. Because of their mass, such diaspores are often dispersed by biotic vectors, although less frequently they may be transported by gravity or water. A large seed provides a massive reserve of nutrients to the young seedling and enables it to become established in the shade of the deep forest. Between the two extremes are groups of plants with intermediate habit, habitat, diaspore, and seed size including (in order of decreasing stature and seed size) woodland shrubs, woodland herbs, and herbs of woodland margins.

It should be noted that this is a general tendency, rather than an invariant rule. Habit and habitat adaptation may interact in a complicated manner and influence seed weight. Several early seral (weedy) trees have seeds as small as those of herbs, but possess a tree habit. However, such species (e.g., *Populus* L., *Betula* L., and *Fraxinus* L. in temperate forests; *Cecropia* Loebl. in the New World tropics) are often fast-growing and short-lived, and tend not to form time-stable, closed communities. Further, other features, including water availability and degree of seasonality, may influence diaspore and seed size (Baker, 1972; Levin & Kerster, 1974), and seed sizes in each ecological class appear to be slightly larger in tropical communities than in temperate ones (Levin, 1974). However, an overview of this variation suggests that the basic pattern of correlation of seed size with the habit and ecology of the parent plant holds as a broad principle in a wide range of environments.

A graphic summary of the average diaspore volume and range of diaspore volume for several modern ecological groups is presented in Figure 2 (cf. Harper et al., 1970). The values for each category were originally calculated by weight (Salisbury, 1942; Levin, 1974), but I have converted this to cubic millimeters by use of the graph presented in Figure 1.

Comparison of the values for the average and range of diaspore volumes (ADV, RDV) for each of these ecological groups with the ADV and RDV for the fossil floras reveals a clear pattern. Cretaceous floras (#1–7) have ADVs equal to or less than that for modern plants of open communities. Further, only in the case of the flora from Massachusetts (#2) does the RDV exceed that seen in modern plants of open habitats. The sedimentary context (Doyle & Hickey, 1976;

Hickey & Doyle, 1977), and the small seeds of the earliest angiosperms, support the contention that they were "weedy" plants of unstable or transient habitats outside of the climax gymnosperm forest (Takhtajan, 1976; Hickey & Doyle, 1977; Doyle, 1978; Niklas et al., 1980; Tiffney, 1981). Note that this statement does not exclude the possibility that the Cretaceous floras included trees, for the ADVs of several Cretaceous floras overlap with the lower end of the range of tree diaspore volumes. However, although trees and shrubs may have been present in these communities, the small sizes of the diaspores involved imply that these were likely early successional plants rather than canopy dominants. An example may be provided by *Platanus* L., which is probably present as early as the Cenomanian (97 Ma) (Dilcher, 1979; Schwarzwaldner & Dilcher, 1981). *Platanus* is an early successional tree in modern floras (Braun, 1950) and has been demonstrated to occupy unstable, stream-side habitats in the Eocene (Wing, 1981).

By contrast, the Tertiary floras possess a wide range of diaspore volumes embracing all five ecological categories of diaspore size. This suggests that each flora has the potential to contain plants of any and all habits and habitats. It is not possible to be certain that any one flora was dominated by plants of a particular habit or habitat from diaspore size for three reasons. First, the diaspore sizes for the five modern ecological categories do overlap. Second, taphonomic factors have resulted in the mixing of disseminules from different communities in the fossil record. Third, the average diaspore volume (ADV) for each fossil flora is not a fully trustworthy indicator of the dominant physiognomy of the community; one or two large fruits can drastically affect the ADV of a flora. For example, the elimination of the three largest diaspores (two species of *Carya* and one of *Juglans*) from the New Haven flora (Fig. 2, #27; $N = 43$ species) drops the ADV from $1,077 \text{ mm}^3$ to 133 mm^3 . The degree of influence of large specimens on the ADV may be approximated by the coefficient of variation (s.d./ $\bar{x}$, see Table 2). Large values of the coefficient of variation indicate that the mean is not that of a randomly distributed population but is an artifact of a polymodal distribution. The value of this coefficient is high through the Tertiary and shows no significant directional change during this time (commencing with the Woolwich and Reading beds, a regression of the coefficient of variation with time yields $P > 0.20$; $r = -0.27$, $N = 18$).

In a broad manner, the ADV decreases through the Tertiary, although not in a statistically-significant manner (regression of ADV versus time yields $r = 0.27$, $N = 18$). The floras (Fig. 2) of the London Clay and Clarno have ADVs very close to that for trees in the modern day. This is not unexpected, as both floras are presumed on taxonomic bases to be related to the modern forests of Indomalaysia (Chandler, 1964). From this high, the ADV falls off through the Tertiary to values close to those for modern plants of open environments (note flora #22, Nowy Sącz, and #24, Kranichfeld). This trend indicates an increasing dominance of smaller-seeded plants and parallels the climatic deterioration and increase in climatic variability that occurred in temperate regions in the later Tertiary (Mai, 1970; Buchardt, 1978). These cooler and more variable temperate climates could be expected to result in the evolution of new, open, unstable communities, populated by plants with a rapid life cycle. This is what is observed in the taxonomic composition of late Tertiary communities, which show a diversification of herbaceous angiosperms (Niklas et al., 1980; Tiffney, 1981). However, it is of great importance to note that while small-seeded forms dominated in the later Tertiary, large-seeded trees remained as part of the flora, although diminished in importance.

In summary, the diaspore size data suggest that Cretaceous angiosperms were small and/or opportunistic plants, and that only in the latest Cretaceous or early Tertiary did the group clearly evolve to include physiognomically-dominant trees of stable, climax forests. This does not exclude angiosperms from forming forests in the Cretaceous, but the diaspore size data suggest that such forests would be restricted to unstable environments, while gymnosperms would be the physiognomic dominants in stable environments. These predictions can be tested in part by examining the sedimentological settings of Cretaceous angiosperm and gymnosperm floras. Angiosperm floras should be more commonly associated with sediments indicative of unstable environments (e.g., river margins), while gymnosperms should be associated with sediments representative of more stable environments (e.g., back swamps or uplands).

The foregoing interpretation rests on at least two assumptions that require consideration. First, does the correlation of diaspore size and habit/habitat witnessed in the modern day hold with respect to Cretaceous angiosperms, for which

there are few modern homologues? I cannot answer this question directly, but suggest that Cretaceous angiosperms do indeed follow the same pattern as modern ones since the relation of diaspore size and habit/habitat holds across a wide range of taxonomic groups. Chaloner and Sheerin (1981) have successfully applied this concept to an explanation of early land plant reproductive strategies, in which the evolution of larger plant size is directly correlated with an increase in disseminule size. Also, while the fact that these Carboniferous plants are extinct makes the inference of successional status tenuous, it appears that the dominants of the relatively more stable lowland swamp communities (e.g., medullosans and certain arborescent lycopods) had larger disseminules than plants of less stable habitats (e.g., calamitaleans, cordaitaleans, and conifers). The Mesozoic flora was dominated by the gymnosperms, members of which had a wide range of diaspore sizes. Some (cycads, araucarian conifers) had quite large seeds that appear to have necessitated biotic dispersal (van der Pijl, 1969), while others had small seeds (some seed ferns, cycadeoids, and taxodioid conifers) morphologically adapted to abiotic dispersal. Retallack and Dilcher (1981) suggested that cycadeoids may have been restricted to unstable stream margins in the Cretaceous, while conifers dominated the more stable upland communities. With the advent of large-seeded angiosperms in the latest Cretaceous and Tertiary, gymnosperms declined in importance (Niklas et al., 1980; Tiffney, 1981). It is unclear if this was an unrelated event or a direct result of the expansion of the angiosperms. The latter possibility deserves consideration, because the dominant modern group of gymnosperms in the Northern Hemisphere are the Pinaceae, which have relatively small seeds and are generally restricted to early successional positions or to sites from which angiosperms are excluded by physiological factors. These elements of circumstantial evidence suggest that the correlation of diaspore size and the habit and/or habitat of the parent plant generally holds for land plants and may be assumed to have done so for early angiosperms.

Second, the association between diaspore size and habit/habitat was demonstrated using temperate plants (Salisbury, 1942; Harper et al., 1970). Does it hold with warm-temperate to often tropical taxa, which commonly occur in the Tertiary? Again, the answer is circumstantial but positive. The relationship of seed size to habit/

habitat of the parent plant seems to be general among land plants, and anecdotal evidence suggests that it holds in the modern tropics (van der Pijl, 1969; Stebbins, 1971; Opler et al., 1980; Janzen & Martin, 1982). In one case where seeds of plants of the five ecological categories were measured (Levin, 1974), the average seed size in each category was a bit larger (two to five times) than observed in the temperate flora. While interesting, the magnitude of this variation is too small to affect the hypothesis of Cretaceous and Tertiary angiosperm seed size presented here.

SEED SIZE AND MODE OF DISPERSAL

Seed (diaspore) dispersal is an important element in the life cycle of seed plants (cf. Levin & Kerster, 1974). Abiotic dispersal (wind, water) is successfully employed by a wide range of angiosperms, including many trees. However, there is little question that biotic dispersal is of greater importance, if not dominant, among angiosperms in the modern day. Biotic dispersal agents exert a strong selective pressure on angiosperm fruit and seed size and morphology, as evidenced by the evolution of a wide range of adaptations for animal dispersal (cf. Ridley, 1930; van der Pijl, 1969). I am unaware of any estimate of the absolute proportion of the world's angiosperm flora that is animal-dispersed, but in the few reports of individual communities, the proportion of biotically-dispersed species is often high (Jones, 1956; Smythe, 1970; Stiles, 1980; Handel et al., 1981) and reaches 90% in some Central American examples (Frankie et al., 1974; Janzen, 1977). This may be affected by edaphic factors, however, as suggested by Janzen's (1977) observation that a low degree of biotic dispersal occurs in some Indomalaysian forests growing on nutrient-poor soils.

There are five animal groups commonly involved in the dispersal of angiosperm fruits and seeds; ants, fish, reptiles, birds, and mammals (including bats). All have, to greater or lesser degrees, affected the size and shape of angiosperm disseminules. The history and general influence of each group is considered in turn.

Ants. Ant dispersal (myrmecochory) is primarily known among forest floor herbs, particularly in the temperate zone (van der Pijl, 1969; Handel et al., 1981) although it is also reported from other areas (e.g., Berg, 1975). Morphological adaptations to ants usually involve small diaspore size and the presence of an oil body or

elaiosome as a food source on the exterior of the diaspore. Although ants are known from the Cretaceous (Burnham, 1978), they would affect only small seeds.

Fish. Fish are generally assumed to have a minor role in the dispersal of angiosperms (Ridley, 1930; van der Pijl, 1969), although a recent study of Amazonian plant communities (Golding, 1980) suggested that fish may disperse diaspores, particularly in time of high water. The degree to which this dispersal syndrome involves adaptations in diaspore morphology and size, and its importance outside the Amazon basin, are not clear. It may not be so much a "coevolved syndrome" as a glorified case of scavenging. Fish have been around since the Paleozoic (Romer, 1966) and may well have served as generalist dispersal agents in swamps and rivers since the Carboniferous.

Reptiles. Reptilian dispersal (saurochory) is a recognized syndrome, often involving brightly colored and odoriferous seeds or fruits borne near the ground and of a wide range of sizes (van der Pijl, 1969). The important modern representatives include turtles and tortoises, which first spread as a group in the Triassic (Romer, 1966), and lizards, particularly iguanas. The latter group appears in the Eocene, although its forerunners may go back to the Upper Jurassic (Romer, 1966). Perhaps the decline of the reptiles at the end of the Cretaceous, just as the angiosperms were undergoing a major expansion, explains the relative lack of dispersal syndromes involving the two groups in the modern day. The possibility must also be entertained that the primary dispersal vectors of the large seeds of the physiognomically-dominant Mesozoic gymnosperms were reptiles, and that the decline of the reptiles may have influenced the demise of some gymnosperm groups in the late Cretaceous (Krassilov, 1978). If so, this would also imply that Late Cretaceous and early Tertiary plant communities were in a state of flux, and open to angiosperm invasion.

Birds. Birds are among the most important of angiosperm dispersal agents, affecting very small to very large diaspores in temperate and tropical communities (Ridley, 1930; van der Pijl, 1969). There are many morphological adaptations of angiosperm disseminules to bird dispersal (ornithochory) because transport may be internal or external. The most common syndrome involves odorless, brightly colored, edible, fleshy fruits with hard, resistant, inner seeds.

These are often clearly displayed; and, in dehiscent fruits, the seeds often dangle from the fruit at maturity.

The fossil record of the birds has been reviewed at the family level by Brodkorb (1971), to which I have added data provided by Kurochkin (1976) (Fig. 3). Bird families often contain organisms of diverse dietary habits, but, based on information provided by van Tyne and Berger (1976), individual families can be described as "carnivorous" (no plant material consumed), "omnivorous" (some plant material consumed), or "vegetarian" (dominantly plant material consumed). Figure 3 presents a summary of the diversity of bird families from the Early Cretaceous to the present, broken into these three dietary groups. No fossil families are included; they are few in number, and it would be difficult to ascertain their dietary affinities. The family level is used for ease of tabulation. A generic or specific level summary is beyond the scope of this paper and would not greatly alter the trends seen in Figure 3, although the family level does mask the effect of the late Tertiary diversification of the species-rich, dominantly omnivorous or vegetarian, passerines (Brodkorb, 1971).

Cretaceous families for which diets may be surmised from modern relatives are predominantly carnivorous and marine; one omnivorous family is present (Cracraft, 1973; Brodkorb, 1976). This conclusion is generally supported by the beak morphology of the fossils. The fossil record of the birds diversifies greatly in the Eocene, and the number of modern families continues to increase throughout the Tertiary. The proportion of omnivores remains steady during this time, but the proportion of vegetarian families (which first appear in the Eocene) rises consistently, while that of the carnivorous families falls.

As displayed in Figure 3, the avian fossil record would suggest that birds were not important in angiosperm dispersal until the early Tertiary, whereupon they became increasingly important and continued to mount in significance to the present day. However, the available fossil record of any group may be seen either as a real reflection of evolutionary events, or as too biased to be trusted directly. Cracraft (1973) considered the fossil record to be less important than the information that can be drawn from a comparison of the timing of Cretaceous and Cenozoic continental movements with the modern distri-

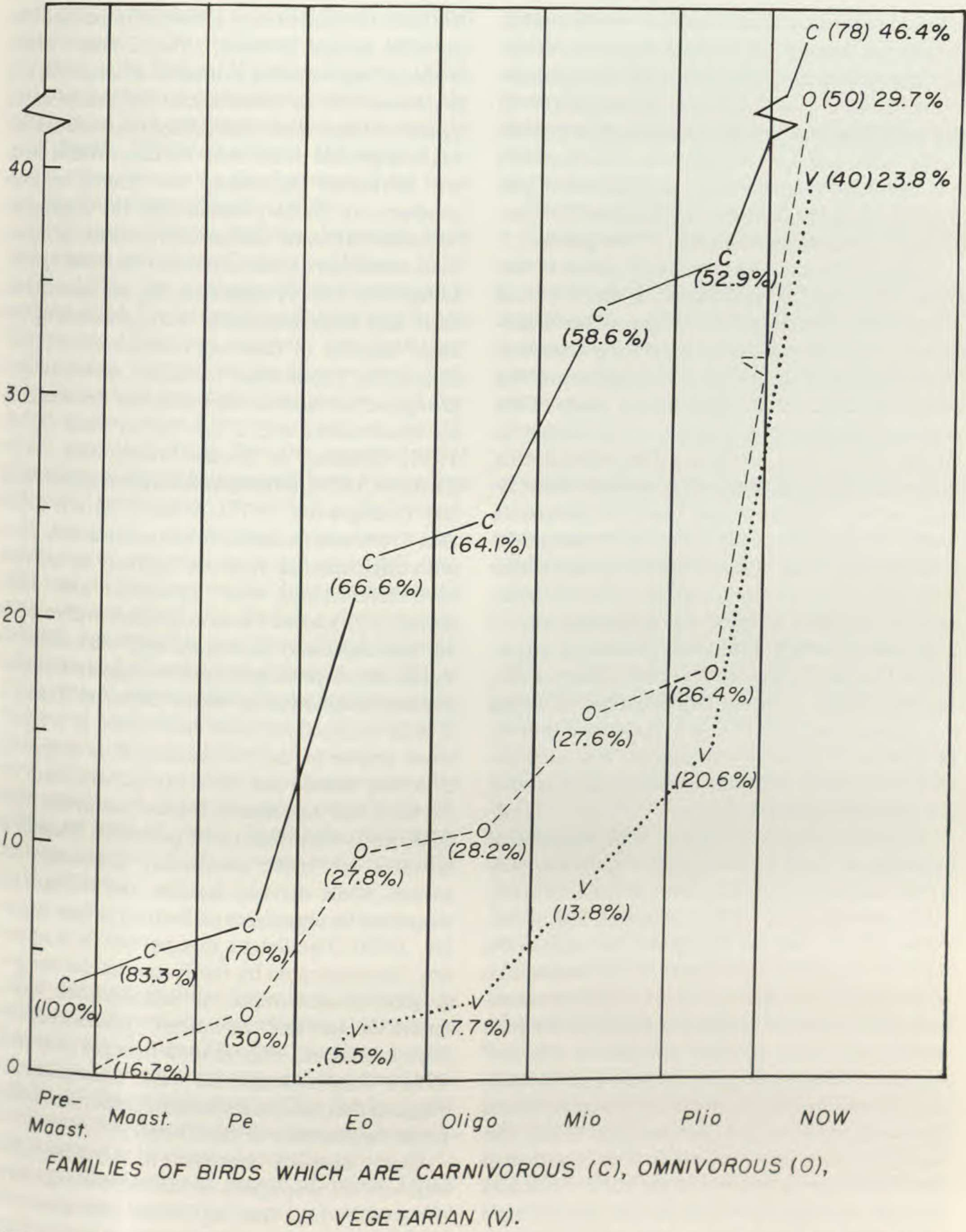


FIGURE 3. Cumulative diversity of modern families of birds through the Cretaceous and Tertiary broken into three dietary groups: carnivorous (c), omnivorous (o), and vegetarian (v). Percentages are of the total number of families in each epoch. Data from Brodkorb (1971, 1976); Kurochkin (1976); van Tyne and Berger (1976). Pre-Maast = pre-Maastrichtian, Maas = Maastrichtian, Pe = Paleocene, Eo = Eocene, Oligo = Oligocene, Mio = Miocene, Plio = Pliocene.

butional patterns of bird families. On this basis, he inferred that the immediate ancestors, if not the actual families, of modern birds were present by the mid- and Late Cretaceous. Brodkorb (1971) also suggested that modern families were present in the mid- and Late Cretaceous. He reasoned that the modern appearance, specialization, and diversity of early Tertiary birds argue for considerable antecedent evolution of the group.

Neither author accepts the fossil record at face value. This logic is reminiscent of the school of paleobotany that sought the origins of the angiosperms in the latest Paleozoic and early Mesozoic on the basis of their "diverse" Cretaceous record (Axelrod, 1960, 1970). Subsequent study of the angiosperms (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Doyle, 1978) has demonstrated that the initial radiation of the angiosperms was confined to the Cretaceous and matches the known fossil record of the group. I choose to accept the fossil record of the birds as indicative of a major radiation in the Tertiary, perhaps with its beginnings in the latest Cretaceous, paralleling that of mammals (Colbert, 1969) and of modern angiosperm families (Niklas et al., 1980; Tiffney, 1981; Muller, 1981). A recent consideration of avian evolution (Cracraft, 1982) does not alter this view, because it emphasizes the aquatic and presumably carnivorous nature of Mesozoic birds as they are presently understood.

Mammals (excluding bats). The dispersal of angiosperm seeds by mammals is probably only a little less important than that by birds (Ridley, 1930; Martin et al., 1951; van der Pijl, 1969; Halls, 1977). Van der Pijl gives the impression that it is of greater importance in the tropics than in the temperate regions. The fruit and seed characters associated with mammal dispersal are quite varied and may involve internal or external transport. Mammals often possess a good sense of smell and thus many mammal-dispersed fruits have a distinctive odor (van der Pijl, 1969). The thickness of the seed wall tends to vary with seed size. Small seeds that would probably be passed through the digestive tract do not require hard coats, whereas large ones with edible contents require protection against direct predation. One important aspect of mammal dispersal is that mammals can move seeds of quite large sizes, often from within the forest canopy (Ridley, 1930; van der Pijl, 1969). Mammal-dispersed fruits of more open habitats are often adapted to external transport (van der Pijl, 1969).

The Tertiary is the "age of mammals," and is

the time of radiation of a host of important dispersalist groups (Romer, 1966; Colbert, 1969). Rodents, lagomorphs, primates, artiodactyls, and perissodactyls all commenced radiations in the Eocene. Other, more specialized omnivorous lineages appeared in the mid-Tertiary. While modern terrestrial mammals are almost entirely products of Tertiary radiations, the possibility remains that some Cretaceous lineages of mammals could have been important dispersal agents. Lillegraven (1979) suggested that perhaps mammals and flowering plants were establishing the basic features of their coevolutionary relationship in the Cretaceous. Certainly, several major groups of Cretaceous mammals are presumed to be omnivorous and a few herbivorous (Kron, 1979; Clemens & Kielan-Jaworowska, 1979; Clemens, 1979), although all are generally of small size (Lillegraven, 1979). While I do not doubt that Cretaceous mammals had some interactions with angiosperms, it seems unlikely to me that such interactions were significant and widespread. The known Cretaceous thick-walled seeds are not especially common, and they show no trends in morphology or size to suggest their specialized adaptation to biotic dispersal. Further, if such interactions were established to a significant degree in the Cretaceous, it is surprising that they should not have carried over into the Tertiary and the present. Instead, today the fruits of primitive families or of primitive lineages in families are more commonly abiotically-dispersed, while derived families and lineages are dispersed by organisms of Tertiary origin (Schuster, 1976). Parallel to this pattern is a second one, demonstrated by the Rosaceae, for the geographic co-occurrence of fleshy-fruited angiosperm lineages and "advanced" (products of Tertiary radiations) mammalian lineages (Schuster, 1976). This information, while circumstantial, suggests that mammals became important as dispersal agents only in the Tertiary.

Bats. Bats are important in the dispersal of angiosperm propagules in the warmer regions of the world where fruiting occurs throughout the year. This is borne out by a wide range of anecdotal and scientific observations (Constantine, 1970; Smith, 1976). Bat-dispersed disseminules are normally large, odoriferous, fleshy fruits with a hard stone, or a similar seed with a sarcotesta or aril (van der Pijl, 1957, 1969).

The fossil record of bats (Smith, 1976) is limited and often fragmentary. Bats first appear in the Early Eocene and possess dentition indicative

of an insectivorous diet. The first frugivorous bat was thought to be *Archaeopteropus transiens* Meschin. of the Italian Oligocene (Jepsen, 1970), but more recent investigation reveals that the dentition of this specimen is that of an insectivore (Smith, 1976). At present, the earliest record of a frugivore is of a phyllostomatid bat from the late Pleistocene (Smith, 1976).

While some authors feel that bats may have been present in the Late Cretaceous (Jepsen, 1970; Smith, 1976), the absence of pre-Eocene bats, and the rapid diversification of the group in the Eocene and Oligocene, suggests that bats were unimportant, if extant, in pre-Eocene time. Further, the earliest bats were insectivores, and frugivory appears to be a derived condition (Smith, 1976). It is thus likely that the morphological characters of the bat-dispersed fruit evolved as a dispersal syndrome at the earliest in the Eocene.

In summary, pre-Tertiary angiosperm dispersal agents probably included ants, fish, reptiles, and certain groups of archaic mammals. Of these, the last group was probably the most significant, but probably was generalized in its adaptations and of restricted influence on the angiosperms. It appears that the important groups of modern biotic dispersal vectors all underwent their most important period of radiation in the early Tertiary. The sudden appearance of such a wide variety of dispersal agents would be expected to lead to clear changes in seed morphology and size. Such changes are seen in the early Tertiary.

CONCLUSIONS

Two separate features have been explored in an attempt to explain the observed pattern of diaspore size change. The first involves the relationship between seed size and the habit and habitat of the parent plant. This leads to the conclusion that the observed increase in diaspore size is related to the angiosperms becoming physiognomically-dominant plants of stable forest communities. The second approach turns to the evolution of dispersal strategies as inferred from the fossil record of the dispersal agents and from the morphology of the disseminules themselves. This suggests that biotic dispersal vectors influenced angiosperm fruit and seed morphology only in the latest Cretaceous or early Tertiary. Each hypothesis provides an adequate explanation of the observed pattern, although the first does not explain its timing. However, the two are not mu-

tually exclusive and may be synthesized to provide a new perspective on angiosperm evolution. As a preamble to this synthetic interpretation, it is necessary to explore briefly the assumption that canopy dominance generally requires large seeds, which, in turn, normally require biotic dispersal agents.

For an angiosperm to achieve dominance (in a physiognomic, not a numerical, sense) of the community, its seedlings must be able to grow in the shade of the parent (or other) trees, thus insuring the continuity of the population. Any increase in seed size in an abiotically-dispersed plant would provide the seedlings with more nutrients and the capability of growing in a more shaded habitat. Logically, one could envision a slow increase in the seed size and shade tolerance of seedlings in one population, ultimately leading to in situ dominance of the community. However, larger seeds generally have a reduced radius of dispersal, particularly in closed communities or in the absence of means of water transport. Thus, in an abiotically-dispersed plant, increased seed size would result in smaller population sizes and perhaps increased endemism and a higher potential for extinction. All this implies that angiosperms required the presence of biotic dispersal agents in order to attain canopy dominance in a closed community. This conclusion appears correct in light of examples of forest trees that have lost their dispersal agents. *Ginkgo* L. attained a wide distribution in the Mesozoic, and maintained it into the Tertiary (Tralau, 1968), but is now a highly restricted endemic in its natural state. Its fleshy and odoriferous seed seems well-adapted to attracting reptiles, and perhaps these were the vectors by which it spread in the Mesozoic. The loss of these vectors in the early Tertiary would be of little immediate importance, because the genus had a wide distribution in this time of warm climate. However, with the climatic changes of the later Tertiary, its range became severely restricted, and, in the absence of a dispersal vector, it was unable to re-expand its range in periods of favorable climate, thus coming to the brink of extinction in the Holocene. Similar, although less dramatic, examples of the effect of the loss of a dispersal agent on range and population structure have been described by Janzen and Martin (1982) for angiosperms in Central America. These circumstantial examples support the tentative conclusion that attainment of canopy dominance and the maintenance of a stable population structure in closed

forests are generally linked to the establishment of biotically-mediated dispersal.

The scenario involving seed size and dispersal in the evolution of the angiosperms is simple. Our understanding of Early Cretaceous land plant communities is limited but conveys the impression that there were few existing seed plants of an early successional nature. The angiosperms first appeared about 120 Ma as an "*r*" strategy (weedy generalist) group with small stature, rapid life cycle, and small, abiotically-dispersed seeds. They spread to occupy a wide variety of early-successional sites (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Doyle, 1978). This diversification was probably paralleled by the appearance of a variety of adaptive vegetative morphologies and may have resulted in the "blocking out" of the general character complexes of several modern suprageneric groups. Evidence from leaf architecture (Doyle & Hickey, 1976; Hickey & Doyle, 1977) indicates that the angiosperms had attained shrub and tree stature by the late Albian or early Cenomanian (about 100 Ma). These plants may have formed extensive angiosperm-dominated communities in consistently unstable environments (e.g., aggradational river bottoms) but probably were displaced by the large-seeded and dominant gymnosperms in more stable habitats. Some angiosperms may have formed an understory of shrubs and small trees in open-canopied gymnosperm forests such as those of the uplands of New Caledonia in the present day (L. J. Hickey, pers. comm.).

Therefore, while Cretaceous angiosperms were probably diverse in certain habitats and perhaps numerically-dominant over the gymnosperms, they did not dominate the world vegetation in the physiognomic sense that they do in the modern day. Rather, they were a more specialized "weedy" group that initially radiated to fill a specific aspect of the community, but that did not continue their radiation at the same rate throughout the Cretaceous. This implies that angiosperm diversity should have risen slowly, rather than dramatically, during the later Cretaceous, which is what is observed (Krassilov, 1977; Niklas et al., 1980; Tiffney, 1981). That the Cretaceous angiosperms included few if any large canopy trees capable of sustaining a closed climax forest is inferred strictly from the paucity of large angiosperm diaspores. While large seeds would have permitted the angiosperms to achieve physiognomic dominance of the community, their size would necessitate association with biot-

ic dispersal agents. Both the record of diaspore size and of animals in the Cretaceous suggest that the appropriate dispersal agents for angiosperms were few, and that the advantages of large seeds were outweighed by the disadvantage of their poor dispersal.

This impasse was broken by the radiation of birds and mammals (including bats) in the early Tertiary or perhaps latest Cretaceous, leading to the swift development of many biotic dispersal syndromes, which in turn influenced the evolution of the angiosperms in the Tertiary.

The total diversity of angiosperms increased dramatically in the early Tertiary (Niklas et al., 1980; Tiffney, 1981). This is to be expected as a result of the development of plant-animal dispersal interactions for three reasons. First, co-evolution favored increasing specialization and speciation (cf. Regal, 1977). Second, greater distance of dispersal favored allopatric speciation, an ultimate example of which is the modern eastern North America-eastern Asia pattern of disjunction (Wood, 1972; Wolfe, 1975). Finally, the establishment of dispersal syndromes with animals opened the way for angiosperms to explore all possible habits and habitats within the community. This is partially reflected in the high value of the coefficients of correlation (Table 2) in the Tertiary, indicating the increased polymodality of diaspore size in Tertiary floras. Increased seed size led to an arborescent community with decreased light penetration, diversified biotic competition, and presumably tighter species packing, all features favoring increased diversity. Further, all the changes in the rate of diversification initiated by the interaction of dispersal agents and angiosperms would both accentuate and be accentuated by parallel co-evolutionary interactions with insect pollinators (Crepet, 1979, 1984).

The latest Cretaceous and early Tertiary is also remarkable as a time of rapid "modernization" of the world's flora. This involves two aspects: the sudden appearance of large numbers of modern families and genera (Niklas et al., 1980; Muller, 1981; Tiffney, 1981) and their swift spread over the Northern Hemisphere (Wolfe, 1975). Both follow logically from the establishment of dispersal relationships. The rapid appearance of modern taxa results from the increased rate of speciation occasioned by the initiation of the co-evolutionary spiral that extends to the present day. The rapid spread of these taxa follows from their association with the effective dispersal

agents, although three other factors were of importance. First, the Late Paleocene and the Eocene were periods of warm climate in the northern hemisphere (Bucharadt, 1978; Wolfe, 1978). Second, apparently both North Atlantic and North Pacific land bridges were available to terrestrial organisms in the Early Tertiary (Lehmann, 1973; McKenna, 1975; Tiffney, 1980). Finally, and perhaps most importantly, the newly-evolved angiosperm taxa probably included many adaptations to previously unfilled "niches" and were spreading at a time when several gymnosperm groups had recently declined or gone extinct (Krassilov, 1978; Niklas et al., 1980; Tiffney, 1981; Vachrameev, 1982).

The question remains: what initiated the increased level of interaction between plants and dispersal agents in the latest Cretaceous and early Tertiary? Did external factors (e.g., the decline of the reptiles) lead to the evolution of new groups of birds and mammals, which in turn spurred angiosperm evolution? Alternatively, did angiosperms (perhaps responding to the appearance of new groups of insect pollinators, Crepet, 1984) begin to diversify first and thereby stimulate the evolution of potential dispersal agents? I do not believe that the data given here will support interpretations of cause and effect, if indeed, such considerations are not rendered irrelevant by the synergistic nature of coevolutionary relationships. Further, while I have emphasized the historical importance of the development of angiosperm dispersal syndromes in this paper, it is only one of three coevolutionary features that must have had a strong influence on the course of angiosperm evolution. Pollination syndromes have perhaps had an even greater influence in view of the vast array of morphological and ethological permutations involved. Indeed, the interactions of angiosperms with modern pollinators may have been established at a slightly earlier date than the interactions with modern dispersal agents (cf. Crepet, 1984). Additionally, interactions between herbivores and plants have not been explored in the fossil record but must also have been of significance (cf. Niklas, 1978).

Finally, I would like to explore briefly three ancillary points.

First, the evidence presented here suggests that the "Durian Theory" (Corner, 1949, 1964) is untenable. The "Durian Theory" assumes that the primitive angiosperm seed was arillate, of moderate size, probably animal dispersed, and was contained in a dehiscent fruit borne of a

large, pachycaulous tree. According to the fossil record of angiosperm seeds, such a combination of characters could have evolved only in the Tertiary, following the establishment of widespread biotic dispersal syndromes. Certainly no evidence is seen of "moderate-sized" angiosperm seeds in the Cretaceous: they are all small. Further, no evidence is seen of widespread animal dispersal in the Cretaceous, or of pachycauly, although the scarcity of Cretaceous angiosperm wood (Wolfe et al., 1975) renders the last a statement based on negative evidence.

Second, the minimum and maximum seed sizes did not appear to have undergone any significant directional change of size during the time period measured. Two regressions were run: (1) the size of the smallest seed of each of the floras examined (Table 2) against time, and (2) the size of the largest seed from each of the Tertiary floras against time. The first regression was not significant ($0.20 > P > 0.10$; $r = 0.29$, $N = 26$); the Rusin-ga flora was excluded on account of its anomalously large "smallest seed"—probably a function of the collection of the flora from surficial lag deposits. In the second case ($N = 18$, $r = 0.40$), the r value is marginally insignificant ($P = 0.10$), however, this figure may be influenced by the temperate adaptations of the source plants of the later Tertiary. This suggests that the two seed classes have achieved some form of balance between the selective features that affect size. The time stability of small seed size implies that the appearance of larger seeds in the early Tertiary did not alter the selective advantage of small seed size in certain environments. This could be further extended to imply that the basic habitats available to smaller-seeded plants have not greatly altered during the history of the angiosperms, although in some times habitats favoring opportunistic forms are less widespread (early Tertiary) than in others (late Tertiary, Pleistocene). With respect to the larger seeds, it appears that there has been no distinct trend of size increase through the Tertiary. This could imply that there is an optimal upper limit for seed size, one that strikes a balance between available endosperm and efficiency of dispersal, and that was achieved by the early Tertiary. However, this observation may be influenced by climate. The fossils are primarily from Europe and sample a tropical vegetation in the early Tertiary, but an increasingly more temperate one through the later Tertiary. Limited data (Levin, 1974) suggest that modern tropical lowland communities have

slightly larger seeds than modern temperate ones. If so, then possibly the size of the largest seeds did increase slightly through the Tertiary.

Finally, both Harper (1961) and Margelef (1968) have suggested that the evolutionary history of a group should tend to parallel its successional history, and that an evolving group should "climb its own seral tree." This is what is seen in the fossil record, with the angiosperms initially appearing as weedy plants and in due time evolving to become dominant members of the climax community. The fossil record suggests that this transition required the appearance of dispersal vectors to permit the dispersal of large seeds of the plants of later seral stages. This implies that the unique characters of the angiosperms (rapidity of life cycle, potential for insect pollination, specialized conducting tissue, etc.) were not sufficient separately or jointly to directly ensure the final dominance of the group. However, the developmental plasticity of the angiosperms did permit them to evolve a diversity of fruit and seed dispersal adaptations in response to the appearance of dispersal agents. This observation raises interesting questions about the structure and function of pre-angiosperm communities. Were dispersal agents involved in previous climax communities? Do climax communities in which dispersal agents are not available have a different, perhaps more open, canopy structure than those in which dispersal agents are present? [For example, could the seeming diversity of lowland Carboniferous coal swamps as contrasted to the upland Carboniferous vegetation be influenced by the availability of mechanisms permitting the dispersal of large seeds in the lowland community (water, fish) and their absence in the upland communities?]

SUMMARY

Analysis of Cretaceous and Tertiary fruit and seed floras from the Northern Hemisphere reveals a change in the average size and range of size of angiosperm diaspores through time. Cretaceous floras are composed almost entirely of small diaspores. Early Tertiary floras are dominated by large diaspores but include many as small as those of the Cretaceous. Later Tertiary floras are primarily composed of smaller diaspores but consistently include a few very large ones. Analyses suggest that the minimum diaspore size for angiosperms has not changed since their appearance in the Cretaceous, and that their

maximum size has not increased greatly, if at all, from the time of appearance of large diaspores in the earliest Tertiary to the present. There are two major features that influence diaspore size: (1) the relation between seed size and the ecological characteristics of the parent plant, and (2) dispersal mechanisms. The observed pattern in angiosperm diaspore size through time may be interpreted in light of these two selective forces. Cretaceous angiosperms were primarily small-seeded, abiotically dispersed shrubs or opportunistic trees, perhaps occupying marginal or open habitats in the gymnosperm-dominated vegetation, but probably not forming a closed-canopy climax community. The relative paucity of dispersal agents in the Cretaceous limited the success of large angiosperm diaspores and the closed-canopy forest that they could be expected to give rise to. The latest Cretaceous or early Tertiary radiation of birds, bats, and terrestrial mammals reversed this situation, permitting a biotic interaction favoring large, animal-dispersed propagules. This in turn allowed the establishment of angiosperm seedlings in areas of low light intensity and led to the development of stable, closed-canopy, climax communities, physiognomically- as well as numerically-dominated by angiosperms, and similar in structure for the first time to those of the modern day. This interaction of seed size and dispersal agents may have occurred with, or slightly later than, the establishment of interactions between angiosperms and modern pollinators. Regardless of sequence, the establishment of biological interactions between angiosperms and their pollinators and dispersers was reflected in the rapid appearance of modern families and genera, and of their swift spread around the northern hemisphere, in the latest Cretaceous and early Tertiary.

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